Reference *Biol. Bull.*, **151**: 344–356. (October, 1976)

FLOW AND FEEDING IN FAN-SHAPED COLONIES OF THE GORGONIAN CORAL, *LEPTOGORGIA*

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Many polypoid suspension feeders are fan-shaped and orient perpendicular to prevailing water currents (Riedl, 1966). Perpendicular orientation of gorgonians has been described as due to hydrodynamic forces (Theodor and Denizot, 1965; Wainwright and Dillon, 1969; Grigg, 1972) and as an adaptation for greater feeding efficiency (Laborel, 1960; Barham and Davies, 1968). It is likely that the mechanical properties of the skeleton and the morphology and orientation of colonies are well-adapted to both feeding and support as stated by Wainwright and Dillon (1969).

The objectives of this study are first, to determine whether morphology and orientation of the sea-whip *Leptogorgia virgulata* can be correlated with prevailing tidal currents; and secondly, to test the hypothesis, in laboratory studies, that fan-shaped colonies oriented perpendicular to flow (Fig. 1) will have a feeding advantage over colonies oriented parallel to flow. Feeding rates are measured by the number of *Artemia* nauplii caught per unit time. The importance of morphology and orientation to the feeding success of passive suspension feeders is examined in light of the data collected.

MATERIALS AND METHODS

Field studies

The morphologies and orientation to currents of two populations of *Leptogorgia* in the vicinity of the Duke University Marine Laboratory, Beaufort, North Carolina, were surveyed using S.C.U.B.A. gear.

Channel population. One population was found in a channel in 5–7 meters of water. The colonies were attached to shell and rubble covered by smooth sand. The dominant hydrodynamic forces in this protected area were due to daily bidirectional tidal currents. A 10 × 2 meter grid was laid out across the bottom of the channel and current speeds and direction were measured at the 0 m, 5 m, and 10 m points across the grid, 0.5 m off the bottom. Current speed was determined by timing the passage of suspended particles across a 1 m distance and was found to range from 0–0.25 m/sec (0–0.5 knots) depending on tidal stage. Current direction was recorded by measuring the compass bearings of fine nylon streamers. Neither current speed nor direction were found to vary significantly across the grid.

Morphology and orientation of colonies within the grid were determined. The degree of planar or fan-shaped morphology is indicated by the thickness to width ratios of 1:5, 1:4, 1:3, 1:2, 1:1 (Fig. 1). A ratio of 1:5 indicates a high degree of fan-shaped morphology, while a ratio of 1:1 indicates that the branches

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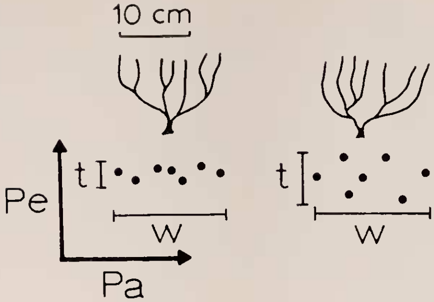

FIGURE 1. Whole fan-shaped colonies as seen upright (top) and as branch tips would appear when seen from above (bottom). Thickness to width ratios (t: w) were calculated as a measure of fan morphology. Orientation to flow is classed as perpendicular (Pe) when flow direction intercepts the fan blade at right angles and parallel (Pa) when flow direction is colinear with width of the fan blade.

are distributed in a bushy, three-dimensional array. Thickness to width ratios were measured from tracings of branch tip positions made on a clear plastic plate positioned above colonies during slack tide. Orientations of planar colonies were measured during slack tide by visual orientation of a protractor to the plane of the colony and are expressed in degrees relative to previously recorded tidal current direction. An orientation of 90° indicates that the fan is perpendicular to the tidal current. Orientations are grouped in 10° classes.

Jetty population. The second population of *Leptogorgia* was found scattered over the surface of a rock jetty at the south-west corner of Piver's Island. This population was attached to rough broken concrete in 1–5 meters of water and was subjected to currents from two converging tidal channels in addition to swell caused by frequent passing of trawlers and pleasure boats. Current speed and direction were monitored at eight locations within a 20 m^2 grid using the methods described. Suspended particles showed turbulent currents with frequently changing speed and direction across the grid and even around single colonies.

Feeding studies

Feeding mechanisms and feeding rates. Fan-shaped colonies of *Leptogorgia* 0.1–0.15 meters in height, were placed in a recirculating water tunnel of 60 liter capacity with a working area 0.3 meter long by 0.2 meter square (Fig. 3). The tunnel was powered by a 1/30 H.P. heavy duty laboratory stirrer connected to a solid state motor control. Current speed was determined by timing with a stopwatch the passage of suspended particles in the center of the working area over a distance of 0.3 meter. The mean of ten determinations was used as the recorded speed, and the results of a typical determination are 0.04 ± 0.005 m/sec. The rpm of the motor were checked each hour during an experiment using a Model 1531 Strobotac (General Radio Co., Concord, Mass.) and were found to be constant ±3%. Plexiglass baffles and a laminator of plastic soda straws (individual straw, 0.25 × 8.25 inch, Sweetheart Straws, Maryland Cup Corp.) maintained a reasonably laminar flow. Except in the boundary layer 2 cm

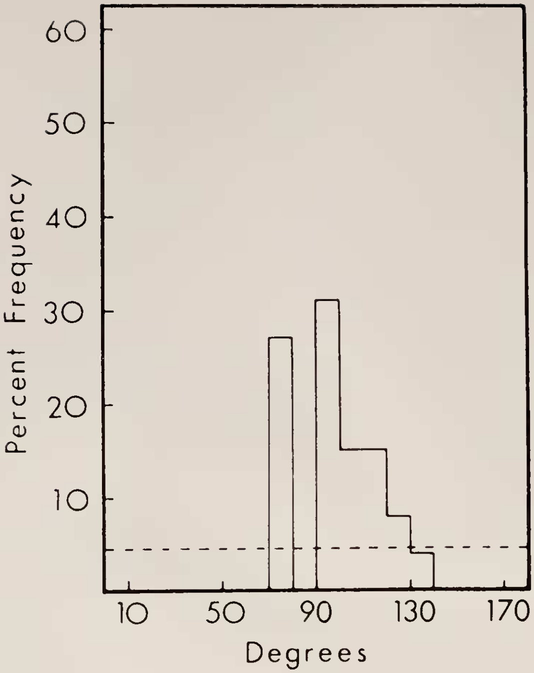

FIGURE 2. Orientation of fan-shaped colonies in the channel population relative to tidal current direction. Colonies are grouped in 10° classes, 90° representing an orientation perpendicular to the current. The probability that the observed distribution is a chance sampling from a random distribution (represented by dotted line) is less than 0.001 ($\chi_{25}^2 = 299$).

thick, working area current velocities were equal to central velocity minus 1–10%. Current velocities in the boundary layer were found to be reduced by up to 50% below central velocity.

The tunnel was filled with sea water filtered through a 5 micron filter bag. Selected fan-shaped colonies were collected and held in filtered sea water for a 24-hour fasting and acclimation period before use. They were then placed in the tunnel oriented either parallel or perpendicular to the current direction and allowed to acclimate further for several hours before *Artemia* nauplii were added. Living *Artemia* nauplii were harvested from culture 24 hours after eggs had been

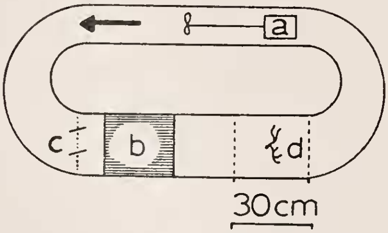

FIGURE 3. Recirculating water tunnel seen from above: lab stirrer (a), laminator (b), baffles (c), and working area with colony (d). Flow direction is indicated by arrow.

added to filtered sea water. *Artemia* carapace length was 0.48 ± 0.03 mm, n = 20. The *Artemia* nauplii were counted by eye using a 10 ml pipet and added to the tunnel until a final concentration of 20 ± 3 per liter was obtained. The number of *Artemia* in the tunnel was determined directly by taking 4–6 one liter samples using a 1000 ml beaker. Samples were pourer through a 47 mm Millipore filter apparatus under gentle aspiration; the cellulose filters were replaced with a square of #20 mesh nylon plankton netting. The *Artemia* nauplii were counted by eye on the netting and returned to the tunnel along with the filtered sea water. Tests showed that *Artemia* so handled survived as well as controls over a 24 hour period. During an experiment, *Artemia* nauplii were sampled every one to two hours over a four to six period.

At the end of each experiment, the colony was removed and held in filtered sea water for 24 hours. It was then returned to the tunnel, which had been drained and refilled, rotated 90° from its orientation in the first experiment. Some colonies were tested first in a perpendicular orientation followed by parallel orientation, and other colonies were tested in reverse order. Altogether twelve orientation-feeding experiments on six different colonies were completed.

Calculation of feeding rates. Feeding rates in this study are expressed as percentage of *Artemia* consumed per colony per unit time rather than the more conventional "clearance rate" for the reasons discussed below.

Active suspension feeders can be defined as those which maintain a feeding current using cilia or appendages. Jørgensen (1949) has shown that in a closed suspension-feeding system, the concentration of food particles will decrease exponentially with time according to the following formula: $\text{conc}_t = \text{conc}_0 \times e^{-(mt/M)}$, where conc_t represents the concentration of particulate food in the system at time t; conc_0 the concentration of food at time 0; M the volume of the tank; m the volume of water "cleared" of food at time t; and e the base of natural logarithms. Calculation of the clearance rate, the volume of water cleared per unit time, is frequently used as an expression of feeding rate in active suspension feeders, and depends on the volume of water pumped and particle retention of catch efficiency (number of particles retained/number of particles encountered). For active suspension feeders, the container can be considered a well-stirred volume, and particle retention will not vary with ambient currents unless current velocities are so high or so low as to interfere with the feeding current generated by the animal or with the distribution of food in the system.

For a passive suspension feeder like *Leptogorgia*, feeding on large particles, ambient currents are analogous to feeding currents or the volume of water pumped by active suspension feeders. As ambient current velocity ("pumping rate") increases, the clearance rates will *increase*. It is apparent from observations, however, that at high current velocity (≥0.5 m/sec) bending of the colony and polyps reduces the likelihood of *Artemia* capture (*i.e.*, above a certain current velocity, particle retention or catch efficiency decreases, with a resulting *decrease* in clearance rate). These counteracting effects of increasing current velocity bring into question the use of clearance rates as a measure of feeding in passive suspension feeders, and point out the need to carefully specify the current regime under which experiments are conducted. The use of colonies in different orientations at similar current speeds and with similar initial *Artemia* concentrations allows the use of

TABLE I

Thickness to width ratios of colonies of Leptogorgia *from two locations. The probability that the frequency of fan-shaped colonies is the same in both locations is less than 0.001* ($x_4^2 = 33.3$).

Fan-shaped morphology	Thickness to width ratio	Number of colonies	
		Channel	Jetty
Excellent	1.5	11	2
Good	1.4	13	4
Fair	1.3	3	3
Poor	1.2	7	6
None	1.1	2	27
		36	42

the simpler percentage of *Artemia* consumed/time as a measure of feeding rate. Feeding rates were calculated from best fit plots of log percentage of *Artemia*/liter *vs.* time in hours, over a period of four hours.

The current velocity chosen (0.04 m/sec) lay within the range of currents measured in field studies and did not cause severe bending of the colonies or polyps. The *Artemia* concentration of 20/liter was high enough to measure reliably using the sampling technique described, but low enough to avoid satiation of the colonies. The estimated number of polyps per colony ranged from 5–20 × 10^3, with the total number of *Artemia* in the tunnel at about 1–1.5 × 10^3. The *Artemia* concentration of 20/liter is 10–20 times higher than the natural zooplankton population in the Beaufort area (W. Kirby-Smith, Duke University, personal communication), but is closer to natural conditions than the 2–3 × 10^3/liter used in previous suspension-feeding experiments (Crisp and Southward, 1961)

RESULTS

Field studies

The data in Table I indicate that there is a much higher incidence of colonies with a low thickness to width ratio in the channel population, subjected to bidirectional currents, than there is in the jetty population, subjected to unpredictable turbulent currents. This result is similar to that of Grigg (1972) who found that colonies of *Muricea* assumed more fan-like morphologies in the presence of strong bi-directional currents.

The fan-shaped colonies of the channel population have a strong preferred orientation perpendicular to the prevailing tidal currents (Fig. 2) Even if the resting orientation deviates some 20–30°, the comparatively spindly *Leptogorgia* is easily twisted into a 90° orientation by currents. When tidal currents were running, fans invariably were oriented perpendicular to current direction indicated by the path of suspended particles. These data support subjective impressions of divers who reported seeing populations of *Leptogorgia* with fan-shaped morphologies and uniform orientation to current direction (R. Searles, Duke University, personal communication). *Leptogorgia,* then, is another example of a gorgonian coral of variable morphology showing a high incidence of fan-shaped colonies oriented perpendicular to directional currents and can be used to test the hypothesis that this orientation confers some feeding advantage.

Feeding studies

Feeding rates of each colony in perpendicular and parallel orientation were calculated from best fit linear regression plots of log # *Artemia*/liter *vs.* time in hours. The semi-log plot (Fig. 4) is an estimate of feeding rate (Jørgensen, 1949). Observed differences in slopes for parallel and perpendicular orientation were tested for significance by analysis of covariance (Snedecor and Cochran, 1967, p. 433). For ease of presentation, feeding rates are presented in Table II as the percentage of *Artemia* consumed/colony/hour.

It can be seen in Table II that in all cases, colonies in a perpendicular orientation capture as many or more *Artemia* per unit time than the same colonies oriented parallel to flow. The range of differences is great and not all differences are

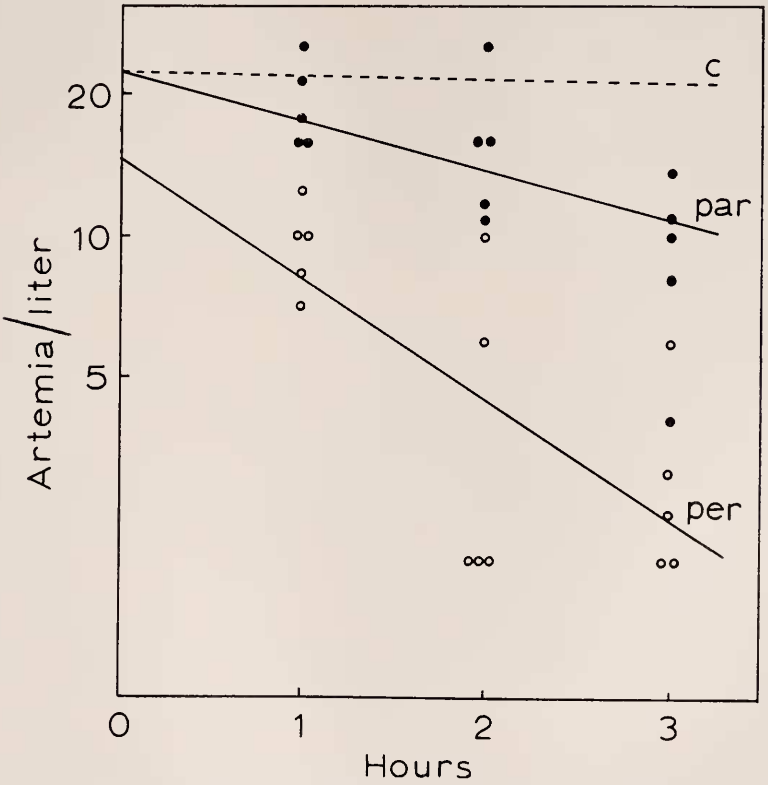

FIGURE 4. Best fit linear regression of log # *Artemia*/liter vs. time for colony #1 water tunnel feeding experiments. Slopes are a measure of feeding rate and are significantly different ($F_{1,36} = 6.36$, $P < 0.05$) for perpendicular orientation (open circles, $y = -0.2594x + 1.6990$) *vs.* parallel orientation (closed circles, $y = -0.1184x + 1.3670$). Experiments in which colonies did not expand are used as controls (C, dashed line) and show no significant loss of *Artemia* over 18 hours.

TABLE II

Feeding rates of fan-shaped colonies in parallel vs. *perpendicular orientation relative to tunnel water current. Feeding rates were calculated from best fit linear regression of log #* Artemia/*liter* vs. *time in hours, and are expressed as %* Artemia *consumed/hour. The significance of feeding rate difference for each colony as determined by analysis of covariance (Snedecor and Cochran, 1967, p. 432) is listed in parenthesis (n.s. = not significant). Experiments are listed in chronological order.*

Colony	Orientation	Feeding rate % *Artemia*/hr	Rate difference perpendicular-parallel
1	Perpendicular	28.5	+ 5.5 (n.s.)
	Parallel	23.0	
2	Perpendicular	39.6	+ 15.6 ($P < 0.05$)
	Parallel	24.0	
3	Parallel	24.5	+ 52.2 ($P < 0.05$)
	Perpendicular	76.7	
4	Parallel	34.5	+ 6.5 (n.s.)
	Perpendicular	41.0	
5	Parallel	38.6	+ 7.0 ($P < 0.05$)
	Perpendicular	45.6	
6	Perpendicular	66.2	+ 43.9 ($P < 0.01$)
	Parallel	22.3	

significant for single experiments, but the trend is clear enough to suggest that the phenomenon is real. For the first time, experimental evidence shows that fan-shaped colonies do have a feeding advantage when oriented perpendicular to flow, regardless of the actual mechanisms which control morphology and orientation. The question of feeding as related to colony morphology is explored in the following discussion.

DISCUSSION

Colonies of *Leptogorgia* in the Beaufort area are typically 0.2–0.3 meters in height, with a maximum height of probably 0.5 meters. The colonies used in feeding studies were 0.1–0.15 meters in height and fan-shaped, *i.e.*, no branch was located downstream of another branch. The polyps on colonies of this size average about 1 mm in length by 0.5 mm in width, with a spread of expanded tentacles of about 1 mm diameter, although these measurements vary greatly with degree of expansion of individual polyps. The spicular coenenchyme axis of each branch when expanded may be 0.5–2.0 mm in diameter, with polyps more or less randomly distributed around the circumference and along the axis of each branch. Some other gorgonian corals have very regular arrangements of polyps, and careful studies of *Leptogorgia* may reveal subtle patterns of polyp distribution which may affect feeding success.

Feeding rate measurements must take into account the willingness of the animal to feed. The assumption that corals with polyps expanded are feeding is not necessarily valid. When an *Artemia* encounters an actively feeding polyp, it will be enveloped by all tentacles within 1–2 seconds and be conveyed to the mouth. An *Artemia* can be ingested within 5 seconds. Ingested specimens of *Artemia* are clearly visible in the gut cavity of individual polyps which have recently fed and can pass from the polyp out of view into the colonial gastrovascular cavity as rapidly as 1–2 minutes. As many as 5 feedings in 30 minutes by one polyp have been observed. The rate of passage of *Artemia* nauplii into the colonial gastrovascular cavity slows with repeated feeding.

There is a great range of individual polyp responses. Some polyps feed repeatedly, some polyps feed once and remain with tentacles contracted, some polyps evidently do not feed at all. Even with polyps fully expanded, it was apparent that a colony may stop feeding. An *Artemia* encounter with a nonfeeding polyp triggers an initial, often incomplete, tentacle response, but ends with polyp tentacles unfolding and the *Artemia* swimming off apparently unharmed. Feeding experiments using branch tips in test tubes show that feeding may stop with as few as 10% of the polyps having fed. Control of the feeding response in *Leptogorgia* and other corals is not understood.

Logic suggests that feeding in passive suspension feeders should be related to current direction and velocity, prey density, size, etc. In these studies, some preliminary evidence was obtained suggesting that colony feeding response is related to changes in current velocity, a 4–6 hour period approximating one tidal period, and changes in prey density.

Observations in the feeding experiments conducted suggest that contracted colonies quickly expand (to feed) when subjected to a current, and that colonies

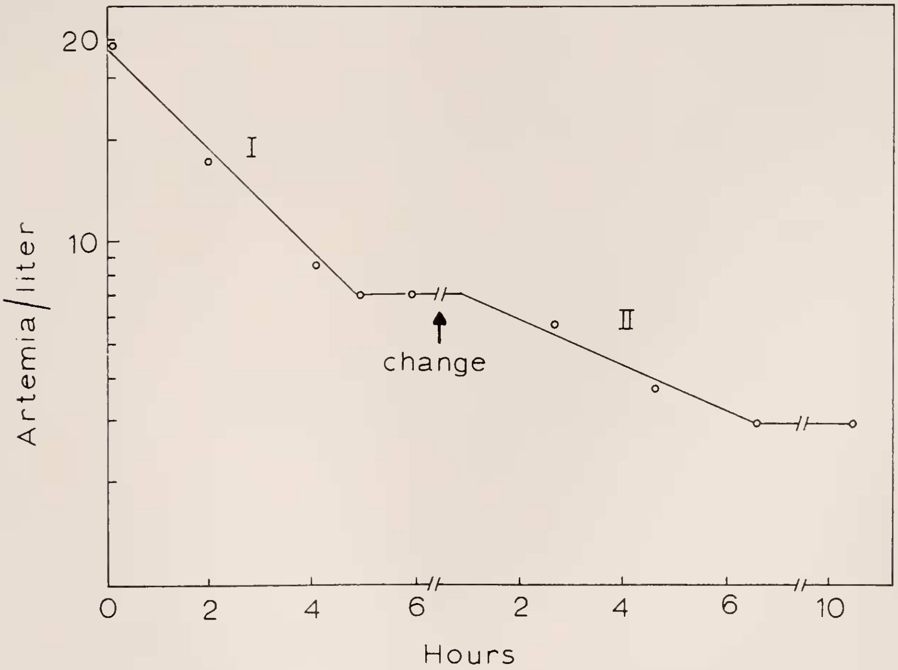

FIGURE 5. Cessation of feeding in two colonies after a 4–6 hour period approximating one tidal flow, regardless of prey density. Colony I fed at an initial *Artemia* concentration of 20/liter, stopped feeding after about 4 hours. Colony II fed for 4–6 hours when placed in the same water at the lower *Artemia* concentration (9/liter). This suggests that feeding may be linked to a 4–6 hour period rather than *Artemia* density. This type of result was found in two separate experiments using four different colonies of approximately the same size.

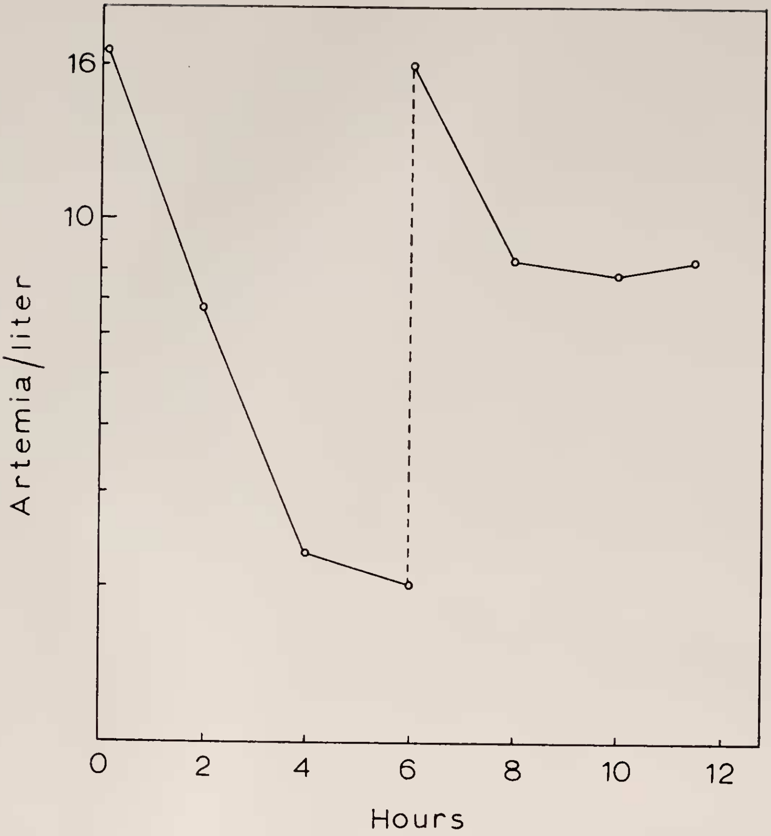

FIGURE 6. Induction of a colony feeding response by increasing *Artemia* concentration to initial levels (16/liter) after cessation of feeding at 4–6 hours. Similar results from two separate colonies suggest, that changing prey density is a factor in determining feeding response.

which contract after a period of exposure to a current tend to expand if current velocity is increased or decreased slightly. This sensitivity to change of current velocity was not tested systematically, but such sensitivity would be a likely mechanism for control of feeding response.

In the feeding experiments conducted, it was also noted that there was a tendency for colonies to stop feeding at 4–6 hours after "time 0" with final *Artemia* concentrations of from 2–5/liter. A single colony fed on four separate occasions at initial *Artemia* concentrations ranging from 20–60/liter, stopped feeding after 4–6 hours despite a range of final concentrations of from 2–25 *Artemia*/liter. This evidence suggests that cessation of feeding response is related to a 4–6 hour period following initiation of current flow and not to final prey density. Further evidence for this conclusion is found in results of two separate experiments which show that after one colony completes its 4–6 hour feeding period, a second colony will feed for 4–6 hours on the remaining prey (Fig. 5).

Experiments on two separate colonies suggest that changes in prey density can stimulate a colony feeding response. In these cases, addition of more *Artemia* at the end of the 4–6 hour feeding cessation induced a new but brief (two hour) feeding response (Fig. 6). This inducible feeding response would be adaptive in feeding on plankton "patches."

It is logical to assume that tidal periodicity, changes in current velocity, or changes in prey density might affect the responses of a passive suspension feeder. It is not clear, however, that any metabolic cost or effort is required for corals to remain constantly in a feeding state. Therefore, it is not clear what advantage is inherent in a periodic nonfeeding state. Perhaps these periodic feeding states, if real phenomena, are related to biochemical processes following a successful feeding period. Clearly, confirmation of these suggested feeding rhythms is in order before speculating further on their possible causes. Additional work in this area must avoid possible satiation effects which might affect feeding periodicity, and could involve careful determinations of prey/polyp ratios for fully fed colonies. These must be determined more carefully than my test tube determined 10–15%, and have their fasting conditions more carefully defined than the arbitrary 24-hour period used in this study.

The distribution of polyps around a branch of *Leptogorgia* seen in cross section is more or less uniform. One would expect only the upstream or side polyps to capture *Artemia*. In fact, downstream polyps catch many *Artemia* nauplii held in eddy currents in the downstream sides of the branches (Fig. 7). *Artemia* naupli may remain in these eddy currents for 15–20 seconds (personal observation). The *Artemia* nauplii swim or are carried by currents up and down the backside of branches and are often caught by feeding polyps. At current speeds in excess of about 0.04 m/sec the side polyps are swept back where they too feed in this eddy current. The generation of eddy currents by a colony may be a significant factor in feeding success.

Although fan-shaped colonies feed more rapidly with their broad surface facing the prevailing currents, the eddy currents noted may contribute to the feeding success of colonies which do not have a planar morphology. In a bushy, three

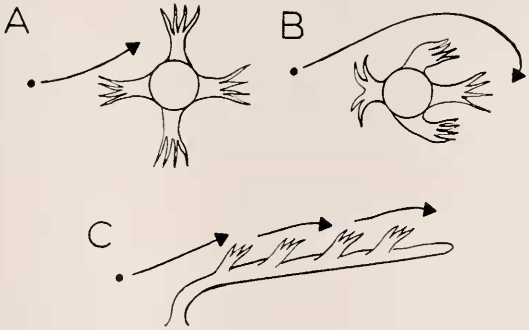

FIGURE 7. The effect of currents on movement of food particles (dot) and polyp position. In A (branch cross section), at current speeds of 0–0.05 m/sec, front and side polyps are at right angles to the branch and catch most prey. In B, at higher current speeds, side polyps tend to be bent back where they feed in eddy currents with rear polyps. In C, at current speeds ≥0.1 m/sec, branches bend over and prey have been seen to bounce from polyp to polyp until caught.

dimensional array of branches, the downstream branches would be feeding in the eddy currents of upstream branches. The colony would thereby have several opportunities to catch a single *Artemia*, compared to the single line of branches in a planar colony. This three dimensional array may catch a very high percentage of the *Artemia* which pass through it, and it remains to be seen whether the greater cross-sectional surface area of a fan-shaped array is actually the most advantageous as far as feeding is concerned.

At higher current speeds (≥ 0.1 m/sec), there is a tendency for colonies to be bent over, and for the polyps to be pressed against the branch surface. The reduced colony area presented to the current and the disadvantageous bending of the polyps would be expected to reduce feeding considerably. This is very likely the case, but *Artemia* nauplii encountering a feeding polyp can be swept away after a brief contact, only to be caught in the gauntlet of polyps downstream (Fig. 7). It is apparent, therefore, that feeding success and feeding "strategy" may change for both planar and bushy colonies at different current speeds, and quantitative data to this effect would be of interest.

In discussing the biological basis and probable selective advantage of a particular morphology and orientation in gorgonian corals, it is important to separate branching pattern effects from effects due to skewed growth patterns. This is especially true when discussing growth mechanisms since the same mechanisms may not be operating in each case.

In general, colony morphology is a result of branching pattern. The distinctly planar morphology of true sea fans, such as the genus *Gorgonia*, is clearly due to the anastomosing pattern of branching in a single plane. This pattern is so consistent as to suggest a close genetic control, such as the genetic determination of alternate *vs.* opposite branching in woody plants. Most gorgonians, however, have a more variable branching pattern and therefore more variable morphology. The planar morphology and orientation of the colony overall is determined as each branch is formed. Grigg (1972) proposes that hydrodynamic forces may be important in determining planar morphology in *Muricea*, but fails to relate these forces to branching pattern. He discusses instead how hydrodynamic forces may affect skewed growth', or warping of branches into a plane.

In fact, there is no data which relates to branching pattern in gorgonians. The high correlation between the presence of directional water currents and the occurrence of planar morphology still does not determine the cause of planar growth form. The processes which stimulate branching at the cellular and organismic level must be understood before the effects of extraorganismic factors can be determined.

Skewed growth due to differential skeletal synthesis is a factor which may affect colony morphology and certainly affects orientation of sea fans.

Wainwright and Dillon (1969) showed that in the genus *Gorgonia* taller sea fans tended to be oriented perpendicular to the prevailing water currents. Smaller colonies were more randomly oriented, reflecting the greater randomness of currents closer to the irregular reef surface. The authors concluded that hydrodynamic forces of prevailing currents twist the randomly oriented fan blades toward a perpendicular orientation such that forces across the fan blade will be equally distributed. The subsequent change in orientation occurs slowly as the fan grows taller and is fixed by differential skeletal synthesis.

Gorgonians with more variable morphologies also seem to exhibit differential skeletal synthesis. As previously noted, the planar morphology and perpendicular orientation to water currents of most gorgonians is primarily due to branching in a single plane. However, some branches arising out of this plane, may show signs of corrective growth or bending. This author has noted this in *Leptogorgia* and Grigg (1972) reported corrective growth in *Muricea*. In gorgonians, it seems that differential skeletal synthesis due to applied physical forces is a mechanism by which an existing skeletal component can be modified in shape or orientation. This mechanism has been reported previously in other skeletal systems, such as bone (Becker, Bassett, and Bachman, 1964) and wood (Kennedy and Farrar, 1965). But this mechanism is distinct from the effect of hydrodynamic forces on branching pattern, a poorly understood phenomenon at best.

This work demonstrates quantitatively that fan-shaped corals oriented perpendicular to water currents have a feeding advantage over fan-shaped colonies oriented parallel to currents. Given these results, it can be stated that this frequently observed fan-shape and orientation is an adaptation for feeding as well as for accommodation to hydrodynamic forces. The degree of bending of colonies at various current speeds may be adapted to maximize feeding while minimizing hydrodynamic drag. Experimental or theoretical investigations into the mechanical properties of the skeletal system as related to feeding and support would be of interest.

If one accepts the importance of colony morphology as a feeding adaptation, comparative studies on the distribution of species or morphological types according to current regime and food type should be encouraged. Evolutionary trends in morphological specialization or generalization as related to feeding in different current regimes can be expected. Most of all, the functional morphology of corals must be seen as a morphology related to flow, and thoughts about corals must be organized in a framework of flowing water.

My special thanks to Steve Wainwright and his research group LIMP, for stimulating my initial interest in corals, and for continued interest, support, and suggestions. My thanks to Bill Bretz for his water tunnel design and his shared ideas and expertise in flows and feeding. Thanks also to John Costlow and the people at DUML for their interest and assistance and to Marcie for putting up with it all. This work was supported in part by a National Science Foundation Summer Postdoctoral Award.

SUMMARY

Field studies demonstrate that the gorgonian coral *Leptogorgia virgulata* assumes a fan-shaped morphology oriented at right angles to prevailing tidal currents. Laboratory studies using a recirculating water tunnel and *Artemia salina* nauplii as food show that fan-shaped colonies oriented perpendicular to water currents capture more *Artemia* per unit time than the same colonies oriented parallel to water currents. Several feeding strategies which may operate at various current speeds are suggested. Possible mechanisms controlling feeding response and

the selective advantage of colony morphology and orientation as related to feeding and resistance to hydrodynamic forces are discussed.

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